

Grazing interactions between a collembolan and fungi in a leaf litter matrix

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With 3 Figures

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1. Introduction

The exploitation of fungal mycelium by Collembola (and other micro-arthropods) is analogous to herbivore grazing in a number of respects (HEAL & MACLEAN, 1976; VISSER, 1985). As with higher plants the fungal food resource is of variable quality according to its age (SHARMA *et al.*, 1977; BURNETT & TRINCI, 1979), growth conditions (LEVI & COWLING, 1969; BOOTH, 1979; DOWDING, 1981) and possibly secondary metabolites (PARKINSON *et al.*, 1979; RICHTER, 1980). These factors influence the selection of different fungal species (VISSER & WHITTAKER, 1977; MARSHALL, 1978; McMILLAN, 1976; NEWELL, 1984a), the selection of high quality food resources within fungal species (LEONARD, 1984a), and hence the growth and reproduction of the Collembola (BOOTH & ANDERSON, 1979).

Field studies on the gut-contents of some Collembola demonstrated seasonal changes (ANDERSON & HEALEY, 1972; TAKEDA & ICHIMURA, 1983). These authors concluded that the Collembola were able to graze epidermal and associated structures of the litter horizon, implying that the internal tissues of the leaf may act as a refuge, albeit transitory, from grazer attack. LEONARD (1984a) showed that Collembola, given the choice, strongly favour high quality and young fungal material, and, given rich nutrient resources, very high consumption rates are possible. The consumption of fungal hyphae by Collembola may be expected to increase nutrient turnover and fungal production by the mobilization of the nutrient pool in senescent tissues. This would maintain the food resource in an active growth phase when moisture and temperature are not limiting microbial activity. However, repression of fungal growth by intense feeding activity has also been reported (HANLON, 1981).

A further analogy with grazing herbivores is that even at the highest feeding intensities when micro-arthropods may consume 60% or more of fungal production (McBRAYER *et al.*, 1974; FRANKLAND, 1975; TADROS & VARNEY, 1983; NEWELL, 1948b), the mycelium is not eliminated from the feeding patch because a component of the biomass is buried within the growth medium.

The availability of fungal hyphae to Collembola, determined by the spatial relationships between the mycelium and its litter resource base in relation to microhabitat access by the animals, is a key to these interactions. LEONARD & ANDERSON (1991) have proposed that an unstable limit cycle between collembola and a fungus growing in defined media on a two-dimensional surface can be stabilised by the introduction of spatial heterogeneity.

This paper further explores the effects of litter architecture on these interactions as a basis for exploring the role of Collembola in nutrient cycling (INESON *et al.*, 1982; VISSER *et al.*, 1981) and shaping microbial communities (VAN DER DRIFT & JANSEN, 1977; NEWELL, 1984a; VISSIER, 1985).

2. Materials and methods

2.0. General note

Experiments were carried out to investigate the effects of Collembola grazing on the distribution of fungal hyphae in leaf litter (Experiment 1) and the dynamics of fungal growth and production (Experiment 2). The same materials and methods were used in both experiments.

2.1. Preparation of the leaf litter

Oak leaf-litter (*Quercus robur* L.) was collected in September from a mature woodland and washed to remove animals, eggs, faecal material and other debris. The midribs were removed and the laminae chibbled to give a 1–2 cm size fraction that was left overnight in distilled water to leach soluble tannins and readily metabolizable substances. After draining, the litter was mixed well and aliquots placed in experimental units of glass bottles (190 ml capacity) containing a base of glass micro-beads (moistened with distilled water) to maintain humidity. The units were incubated at room temperature within trays filled with moist sand and enclosed in large polythene bags.

After four weeks had elapsed to permit the development of a decomposer flora, five units were destructively sampled to determine initial litter dry mass and fungal standing crop and ten Collembola – *Folsomia candida* (WILLEM) – were added to the grazing units. Subsequent sampling was carried out at two weekly intervals, five units per treatment being assayed each time.

2.2. Culture, addition and enumeration of Collembola

The Collembola were maintained and dispensed as previously described (LEONARD 1984a): Animals were only added once to each experimental system and the population was allowed to develop freely over time.

A series of grazed and ungrazed units was destructively sampled each monitoring period to enumerate the Collembola and quantify the fungal standing crop. The former were assessed and grouped as described in LEONARD (1984b).

2.3. Determination of fungal standing crop

Fungal standing crops were determined in litter samples using a modification of the method described by HERING & NICHOLSON (1984).

The litter fragments were left overnight in a bleaching solution (0.3 g sodium chloride in 40 ml distilled water, acidified by the addition of 0.5 ml 10% acetic acid solution), washed thoroughly and then stained with phenolic aniline blue. Finally the fragments were dehydrated in successive changes of alcohol and cleared in methyl salicylate producing transparent leaf tissues in which the stained hyphal lengths could be easily enumerated using phase-contrast microscopy (FRANKLAND, 1974), using the intersection method of OLSON (1950). Ten fields per fragment and twenty fragments per experimental unit were counted on each occasion at a magnification of $\times 400$. In the first experiment, estimates of hyphal lengths were partitioned by altering the focal plane of the microscope and counting hyphae present on the upper and lower leaf surfaces, and within the leaf tissues. This procedure was extremely time consuming and the location of the fungal hyphae was not determined in the second experiment.

Hyphal lengths were converted to a mass basis using the factors given by FRANKLAND *et al.* (1978) and corrected to $\text{mg} \cdot \text{g}^{-1}$ dry mass of leaf-litter.

The occurrence of Basidiomycete fungi was estimated by enumerating those hyphae possessing clamp connections, although it is recognised that the Basidiomycete component may be underestimated as the frequency of clamp connections varies between species.

2.4. Gut-content analysis

The quantitative method described by ANDERSON & HEALEY (1972) and McMILLAN & HEALEY (1971) was adopted for this study.

The Collembola retrieved from the units by flotation were killed and fixed in 70% alcohol. They were then transferred to 0.1% lactic acid for 12 hours, at which point the gut-contents were clearly visible and could be dissected out using fine needles. The contents were then dispersed in a small volume of distilled water with a Pasteur pipette.

The separated and suspended gut-contents were stained with a drop of phenolic aniline blue and then gently deposited by vacuum filtration (water-jet pump), onto the surface of a 'Millipore' filter (mean pore size = 0.22 μm ; filtration area of 7.07 mm^2). The suspension was slowly drawn through the apparatus to prevent disturbance of settlement by turbulence. The filter was sucked as dry as possible, removed, air dried to prevent curling and mounted between slide and cover-slip in DPX mountant; this rendered the filter almost transparent. The amount of fungal material was estimated using the method described above and was corrected to mg per gut. Observations on feeding Collembola, using 'pulses' of a dark coloured fungus whilst feeding them hyaline fungi, showed the proportion of the gut contents representing a day's feeding activity. It was also noted that at any point in time only 70% of the animals appeared to be feeding; the remainder were in a non-feeding phase associated with moulting activities (JOOSSE & TESTERINK, 1977). The numbers of Collembola recovered alive were corrected to numbers g^{-1} dry mass litter so that the amount of fungal standing crop consumed by the resident population of grazers between sampling dates could be determined using the above information.

3. Results

3.1. Partitioning the fungal standing crop in leaf litter

The locations of fungal standing crops in grazed and ungrazed systems (Experiment 1) are shown in figure 1. At no point during the experiment were significant levels of fungal hyphae noted within the internal tissues of the leaves; therefore all further measurements relate to epidermal colonists. The standing crop on the lower (abaxial) surfaces peaked in the absence of grazers at week 6; it then gradually declined. This pattern was reflected in

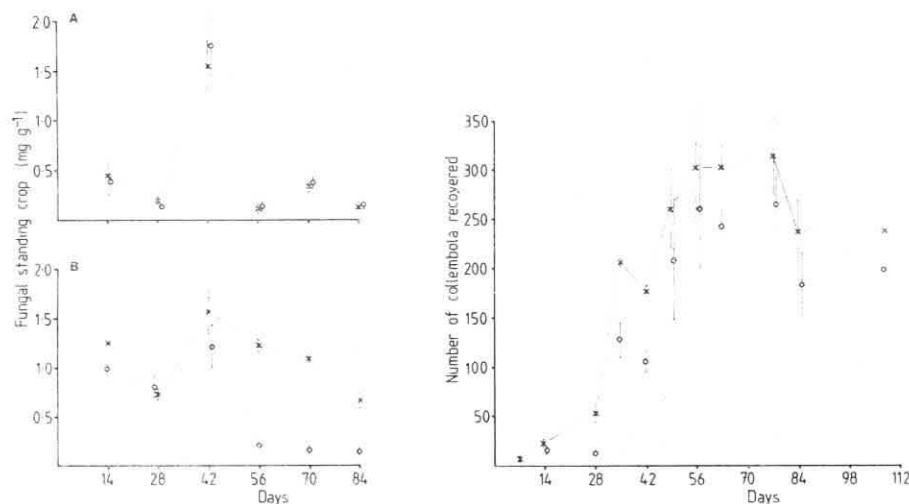


Fig. 1. Fungal standing crops (mg dry mass) present on the (A) adaxial (epiphyllous) and (B) abaxial (hypophyllous) surfaces of the litter recovered from grazed [○] and ungrazed [×] units. Results are expressed as mean values g^{-1} dry mass litter \pm 1 SE (Error bars may be obscured by the symbols).

Fig. 2. Changes in the total number [×] and the number of young [○] Collembola recovered alive from the grazed units. Results are expressed as mean values g^{-1} dry mass litter \pm 1 SE.

the grazed units but the levels were not. By the sixth week recoveries were lower and the subsequent decline was more marked. The growth responses on the upper (adaxial) surfaces were more pronounced, with a distinct peak of standing crops in both the grazed and ungrazed units over weeks 4 to 8 but; unlike the lower leaf surface there was no evidence of any grazing effect.

3.2. The effect of grazing on fungal growth

The Collembola bred freely in the experimental chambers and numbers increased rapidly after week 4 and remained stable over the ensuing 6 weeks (see fig. 2.), although there was some evidence of a slight decline to a lower level by week twelve. A maximum of 300 individuals g^{-1} dry mass litter was attained. One week after the addition of the Collembola the mass of fungal hyphae was 20% greater than in their absence (fig. 3.). However, after a further week the fungal standing crop had declined markedly, whilst that in the ungrazed units continued a gradual increase until weeks four to five. On week six there was a significant drop overall in recovery. After a further four weeks of stable levels, with grazed levels running 70% below the ungrazed, there was a second, substantial increase in both series. Analysis of the fungal material showed that a major production was now an expanding population of Basidiomycete fungi; very few hyphae possessing clamp connections were detected prior to week ten.

3.3. Gut-content analysis

Gut-content analysis from each size class of collembolan showed that all sizes were actively grazing hyphae as follows:

Large (> 1.5 mm length) = $2.12 \times 10^{-4} \text{ mg d}^{-1}$
 Medium (0.5–1.5 mm length) = $1.42 \times 10^{-4} \text{ mg d}^{-1}$
 Small (< 0.5 mm length) = $0.78 \times 10^{-4} \text{ mg d}^{-1}$

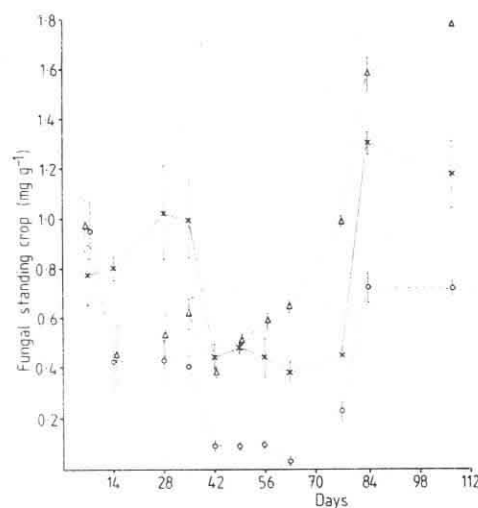


Fig. 3. Total fungal standing crop (mg) colonising leaf litter from grazed [○] and ungrazed [×] units and the grazed fungal standing crop plus that consumed [△]. Details as figures 1A + B.

By correcting the numbers of Collembola recovered from the cultures to density of animals g^{-1} dry mass of litter, and knowing rates of consumption for each size class of animal, cumulative consumption of fungal material was estimated. These estimates of consumption were then added to the observed standing crops to give a value for total production (fig. 3).

The total production curve could not initially explain the deficit between the two series and this reflects other features of grazing over and above direct consumption. However, levels gradually increased until, by week six, the potential standing crop equalled that recovered from the ungrazed systems and by week sixteen the grazer population had consumed almost as much material as was present in their absence. However, in the absence of further information regarding the inflection in the graph no extrapolation was possible as to the potential relationship between consumption and production, especially as the slower growing Basidiomycetes were now a significant proportion of the fungal crop.

4. Discussion

Contrary to our expectations, penetration and invasion of the leaf tissues, which would establish a grazing refuge for the fungus, did not occur. However, partitioning the fungal standing crop on the leaf surfaces showed that the feeding activities of the animals appeared to be completely restricted to material colonising the abaxial surface. Several groups of soil arthropods have been shown to attack litter by removing the lower epidermis and mesophyll from the regions between the finest veins. This produces a characteristic pattern when feeding on leaves of *Quercus* and *Fagus* which has been called 'Fensterfrass' by SCHALLER (1962) (see also NOORDHAM & VLIJGER, 1943) but the reasons why lower surfaces are preferentially attacked are unclear.

Literature regarding the characteristics of fungi within the different environments of the phylloplane is sparse. LAST & DEIGHTON (1965) partitioned fungal colonists and found that some species were restricted to one of the two surfaces. RUINEN (1961) had shown that some species possessed lipase activity, which could enable them to become embedded in the thick waxy layers of the adaxial surface and might therefore prove difficult to dissociate from the cuticle by the animals. Two distinct types have been described; the 'fumagoid' colonies and hyphal colonies (RUSCOE, 1971) revealing adaxial and abaxial tendencies respectively. The 'fumagoid' colonists refer to moulds having conspicuous black, superficial growth forms with closely packed hyphae. Several species have been isolated and described (see FRIEND, 1965a, b) and work may show these colonists to be unpalatable to Collembola as well as difficult to access.

From this study it is apparent that the Collembola were only accessing about half the available fungal standing crop, with estimated consumption rates being 0.8 and 1.1% of dry body mass d^{-1} for the large and medium size classes respectively. These figures fall low in the range (averaging about 7%), reported by MCBRAYER & REICHLER (1971) and others (HEALEY 1967; PETERSON & LUXTON, 1982). Fungivore grazing can therefore account for a significant part of microbial production in the litter. In this study the Collembola rapidly depleted the fungal standing crop as fungal biomass was converted to collembolan biomass. Using a nitrogen model INESON *et al.* (1982) showed that 30% of the nitrogen lost from the fungal biomass was transferred to the grazer population whilst a major proportion of the remaining 70% was attributed to an increase in bacterial numbers. The work of HANLON & ANDERSON (1979) showed that grazing can cause a switch in microbial dominance; however the type of response is a function of grazing intensity (HANLON, 1981). Although, as with this present study, the microbial standing crop present on comminuted and faecal material was not quantified, it is obvious that a figure lower than 70% must be considered realistic as there is strong evidence for nutrient turnover within the fungal biomass. After the initial dip in standing crop, the cumulative plots suggest that although there was no evidence of any stimulation of fungal production by grazing, the Collembola

were harvesting the production and recycling the nutrients through the dissolution of fungal tissues, especially the labile nutrient pool locked up in old and senescent tissues (ENGELMANN, 1961).

In contrast to these results, BENGTSOON & RUNDGREN (1983) observed an over-compensatory growth response by the fungus *Mortierella isabellina* growing in a soil matrix. The accessibility of the fungal mycelium to the animals may be a key factor in these different responses as has been experimentally demonstrated in synthetic two-dimensional and three-dimensional matrices by LEONARD & ANDERSON (1991).

It is difficult to draw any firm conclusions about the catalytic role of Collembola grazing on fungal growth in soil and because little information is available on the importance of these localised effects on the mycelial complex.

Within these experimental systems grazing levels were sufficient to turn over the nitrogen pool sustaining both components of the interaction. However, whether the root/mycorrhizal complex could scavenge the mobilized nitrogen is difficult to ascertain as this must be a function of diffusion distance and potential disruption of mycorrhizal hyphae. Furthermore, studies have shown that there is a non-linear response to grazing intensity, akin to that found by HANLON (1981), with low intensities optimising growth of the external mycelium (FINLAY, 1985), whilst higher intensities render the association ineffective (WARNOCK *et al.*, 1982).

5. Acknowledgements

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6. References

- ANDERSON, J. M., & I. N. HEALEY, 1972. Seasonal and inter-specific variations in major components of the gut contents of some woodland Collembola. *Journal of Animal Ecology* **41**, 359–368.
- BENGTSOON, G., & S. RUNDGREN, 1983. Respiration and growth of a fungus, *Mortierella isabellina*, in response to grazing by *Onychiurus armatus* (Collembola). *Soil Biology and Biochemistry* **15**, 469–473.
- BOOTH, R. G., 1979. The nutritional importance of microorganisms in the diet of soil microarthropods. Unpublished PhD, University of Exeter, UK.
- BOOTH, R. G., & J. M. ANDERSON, 1979. The influence of fungal food quality on the growth and fecundity of *Folsomia candida* (Collembola: Isotomidae). *Oecologia (Berlin)* **38**, 317–323.
- BURNETT, J. H., & A. P. J. TRINCL (eds.), 1979. Fungal walls and hyphal growth. Symposium of the British Mycological Society. Cambridge University Press, Cambridge, UK.
- DOWDING, P., 1981. Nutrient uptake and allocation during substrate exploitation by fungi. In: D. T. WICKLOW & G. C. CARROLL (eds.), *The Fungal Community, its organization and role in the ecosystem*. Marcel Dekker Inc, New York, pp. 621–635.
- DRIFT, J. VAN DER, & E. JANSEN, 1977. Grazing of springtails on hyphal mats and its influence on fungal growth and respiration. In: U. LOHM & T. PERSSON (eds.), *Soil organisms as components of ecosystems*. Bulletin of the Ecological Research Commission (Stockholm) **25**, 203–209.
- ENGELMANN, M. D., 1961. The role of soil arthropods in the energetics of an old field community. *Ecological Monographs* **31**, 221–237.
- FINLAY, R. D., 1985. Interactions between soil micro-arthropods and endomycorrhizal associations of higher plants. In: A. H. FITTER, D. ATKINSON, D. J. READ & M. B. USHER (eds.), *Ecological interactions in soil: Plants, Microbes and Animals*. pp. 319–331. Blackwell Scientific Publications, Oxford.
- FRANKLAND, J. C., 1974. The importance of phase-contrast microscopy for estimation of total fungal biomass by the agar-film technique. *Soil Biology and Biochemistry* **6**, 409–410.
- 1975. Fungal decomposition of leaf litter in a deciduous woodland. In: G. KILBERTUS, O. REISINGER, A. MOURNEY & J. A. CANCELA DA FONSECA (eds.), *Biodegradation et Humification*, pp. 33–40. Pierron Editeur, Sarreguemines.

- D. K. LINDLEY & M. J. SWIFT, 1978. A comparison of two methods for the estimation of mycelial biomass in leaf litter. *Soil Biology and Biochemistry* **10**, 323–333.
- FRIEND, R. J., 1965a. A study of sooty mould on lime trees (*Tilia × vulgaris*). *Transactions of the British Mycological Society* **48**, 367–370.
- 1965b. What is *Fumago vagans*? *Transactions of the British Mycological Society* **48**, 371–375.
- HANLON, R. D. G., 1981. Influence of grazing by Collembola on the activity of senescent fungal colonies grown on a media of different nutrient concentration. *Oikos* **36**, 362–367.
- & J. M. ANDERSON, 1979. The effects of collembola grazing on microbial activity in decomposing leaf litter. *Oecologia (Berlin)* **36**, 93–99.
- HEAL, O. W., & S. F. MACLEAN, JR., 1975. Comparative productivity in ecosystems: secondary production. In: W. H. VAN DOBBEN & R. H. LOWE-McCONNELL (eds.), *Unifying concepts in Ecology*. Dr. W. Junk B. V. Publishers, The Hague. pp. 89–108.
- HEALEY, I. N., 1967. The energy flow through a population of soil Collembola. In: K. PETRUSEWICZ (ed.), *Secondary productivity of terrestrial Ecosystems*. Warsaw. pp. 695–704.
- HERING, T. P., & P. B. NICHOLSON, 1964. A clearing technique for the examination of fungi in plant tissue. *Nature* **201** (4922), 942–943.
- INESON, P., M. A. LEONARD, & J. M. ANDERSON, 1982. Effect of collembolan grazing upon nitrogen and cation leaching from decomposing leaf litter. *Soil Biology & Biochemistry* **14**, 601–605.
- JOOSSE, E. N. G., & G. J. TESTERINK, 1977. The role of food in the population dynamics of *Orchesella cincta* (LINNE) (Collembola). *Oecologia (Berlin)* **29**, 189–204.
- LAST, F. T., & F. C. DEIGHTON, 1965. The non-parasitic microflora on the surfaces of living leaves. *Transactions of the British Mycological Society* **48**, 83–89.
- LEONARD, M. A., 1984a. Observations on the influence of culture conditions on the fungal preference of *Folsomia candida* (Collembola: Isotomidae). *Pedobiologia* **26**, 369–372.
- 1984b. Spatio-temporal interactions between collembola and fungi. Unpublished PhD. University of Exeter, UK.
- & J. M. ANDERSON, 1991. Grazing interactions between a collembolan and fungi in a laboratory matrix. *Pedobiologia* **35**, 163–173.
- LEVI, M. P., & E. B. COWLING, 1969. Role of nitrogen in wood deterioration. VI. Physiological adaptation of wood-destroying fungi to substrates deficient in nitrogen. *Phytopathology* **59** (1), 460–468.
- MARSHALL, V. G., 1978. Gut-content analysis of the collembolan *Bourletiella hortensis* (FITCH) from a forest nursery. *Revue d'Ecologie et de Biologie du Sol* **15** (2), 1–21.
- MCBRAYER, J. F., & D. E. REICHLE, 1971. Trophic structure and feeding rates of forest soil invertebrate populations. *Oikos* **22**, 381–388.
- & M. WITKAMP, 1974. Energy flow and nutrient cycling in a cryptozoan food web. EDFB-IBP 73–78. ORNL: Oak Ridge Tenn. USA.
- McMILLAN, J. M., 1976. Laboratory observations on the food preference of *Onychiurus armatus* (TULLB.) GISIN (Collembola: family Onychiuridae). *Revue d'Ecologie et de Biologie du Sol* **13** (2), 353–364.
- & I. N. HEALEY, 1971. A quantitative technique for the analysis of the gut contents of Collembola. *Revue d'Ecologie et de Biologie du Sol* **8**(2), 295–300.
- NEWELL, K., 1984a. Interactions between two decomposer Basidiomycetes and a collembolan under Sitka spruce: distribution, abundance and selective grazing. *Soil Biology and Biochemistry* **16**, 227–233.
- 1984b. Interaction between two decomposer Basidiomycetes and a collembolan under Sitka spruce: grazing and its potential effects on fungal distribution and litter decomposition. *Soil Biology and Biochemistry* **16**, 235–239.
- NOORDAM, D. Jr., & S. H. VAN DER VAART DE VLIET, 1943. Een onderzoek naar samenstelling en betekenis van de fauna van eikenstrooisel. *Nederlandsche. Boschb. Tijdschr.* **16**, 470–492.
- OLSON, F. C. W., 1950. Quantitative estimates of filamentous algae. *Transactions of the American Microscopical Society* **59**, 272–279.
- PARKINSON, D., S. VISSER & J. B. WHITTAKER, 1979. Effects of collembolan grazing on fungal colonization of leaf litter. *Soil Biology and Biochemistry* **11**, 529–535.
- PETERSEN, H., & M. LUXTON, 1982. A comparative analysis of soil fauna populations and their role in decomposition processes. *Oikos* **39**, 287–388.
- RICHTER, K. O., 1980. Evolutionary aspects of mycophagy in *Agriolimax columbianus* and other slugs. In: D. L. DINDAL (ed.), *Soil Biology as Related to Land Use Practices. Proceedings of the VII International Colloquium of Soil Zoology*, pp. 616–636.
- RUINEN, J., 1961. The phyllosphere. I. An ecologically neglected milieu. *Plant and Soil* **15**, 81–109.

- RUSCOE, Q. W., 1971. Mycoflora of living and dead leaves of *Nothofagus truncata*. Transactions of the British Mycological Society **56**, 463–474.
- SCHALLER, F., 1962. Die Unterwelt des Tierreiches. Springer-Verlag, Berlin.
- SHARMA, P. D., P. J. FISHER & J. WEBSTER, 1977. Critique of the chitin assay technique for estimation of fungal biomass. Transactions of the British Mycological Society **69** (3), 479–483.
- TADROS, M. S., & E. A. VARNEY, 1983. The interrelation between soil arthropods and soil fungi in woodland and field soils. In: Ph. LEBRUN, H. M. ANDRE, A. DEMEDTS, C. GREGOIRIE-WIBO & G. WAUTHY (eds.), Proceedings VIII International Soil Zoology Colloquium, pp. 247–252. Ottignes-Louvain-la-Neuve.
- TAKEDA, H., & T. ICHIMURA, 1983. Feeding attributes of four species of Collembola in a pine forest soil. Pedobiologia **25**, 373–381.
- VISSER, S., 1985. The role of the soil invertebrates in determining the composition of soil microbial communities. In: A. H. FITTER, D. ATKINSON, D. J. READ & M. B. USHER (eds.), Ecological Interactions in Soil, pp. 297–317. Blackwell Scientific Publications, Oxford.
- & J. B. WHITTAKER, 1977. Feeding preferences for certain litter fungi by *Onychiurus subtenax* (Collembola). Oikos **29**, 2–320–325.
- & D. PARKINSON, 1981. Effects of collembolan grazing on nutrient release and respiration of a leaf litter inhabiting fungus. Soil Biology and Biochemistry **13**, 215–218.
- WARNOC, A. J., A. H. FITTER & M. B. USHER, 1982. The Influence of a springtail *Folsomia candida* (Insecta, Collembola) on the mycorrhizal association of leek *Allium porrum* and the vesicular-arbuscular mycorrhizal endophyte *Glomus fasciculatus*. New Phytologist **90**, 285–292.

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The dynamics of interactions between fungi and Collembola in leaf litter were studied under laboratory conditions. Grazing depressed the fungal standing crop on litter by up to 70%. Little fungal development occurred within the leaf matrix and grazing only occurred on the abaxial (lower) surface of the leaves.

The amount of fungal material eaten by different size-classes of Collembola was determined and the consumption by the population was calculated. The comparison of fungal standing crop in the ungrazed litter with the potential level in the grazed litter, calculated by adding the ingested biomass to be remaining hyphae, showed that the Collembola were continually harvesting fungal production. There was no evidence, however, that grazing caused a compensatory growth response by litter fungi in these systems.

Key words: Grazing, Collembola, litter, fungi, growth response, spatial patterns.

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